# DESERT AND LAVA-DWELLING MICE, AND THE PROBLEM OF PROTECTIVE COLORATION IN MAMMALS

By Francis B. Sumner

[*Plate 6*]

The prevailing tendency of desert animals—particularly the mammals, birds and reptiles—to assume a buff or pallid hue is a phenomenon which has long attracted the attention of naturalists. In many cases these colors harmonize strikingly with those of the bare sand and gravel, as well as with the commonly parched and stunted vegetation amid which such animals dwell. Oftentimes the creature need only come to rest in order to disappear from view, its presence becoming evident only when running or flying is resumed.

At a first glance it would seem perfectly evident that we here have to do with the well-known phenomenon of concealing coloration. This, we might suppose, has been acquired by these various creatures through the process of natural selection. The vegetable feeders among them have become more and more invisible to their carnivorous pursuers, while the latter have profited in being concealed from their prey. It is commonly assumed by those who hold this view that the color variations which are selected for survival are quite random in their origin, at least to the extent that they are not influenced in any direct way by the environment.

Various facts make it evident that this explanation is quite inadequate in the case at hand. I will mention but a few of the more obvious objections here. Later, I shall discuss certain special lines of evidence, based upon my own field and laboratory observations.

(1) Most desert rodents are strictly nocturnal in their habits. (This, admittedly, is not a conclusive argument, since the moonlight of the desert is brilliantly clear, and it is probable that owls, at least, among the predators, are largely guided in their search for prey by sight.)

(2) One group of these rodents—the pocket gophers—spend practically their whole time beneath the ground. Nevertheless, strikingly pale species are to be found in certain desert regions. (Here again, it must be admitted that carnivorous animals, both birds and mammals, lay a heavy toll upon the gophers, catching them frequently when they are half emerged from their holes.)

(3) The process of depigmentation applies to parts of the body which are not exposed to view. For example, the soles of the feet of

desert deer-mice are nearly or quite lacking in pigment, while those of mice from the more humid coastal regions vary from purplish to nearly black. Again, the fur of the ventral surface of the body is whiter, in desert forms, owing to the relatively greater length of the terminal unpigmented zone of the individual hairs. Akin to this is the fact that the ventral white area of the pelage tends to extend higher upon the sides of the body, a circumstance which would seem to render the animal more, rather than less conspicuous.

(4) The dorsal white stripes of the skunk are broader in the desert races.[1] It has rarely been contended that the skunk owes its peculiar fur pattern to the need for concealment. The class of facts cited in the last two paragraphs seems to indicate that depigmentation, rather than concealing coloration *per se*, is the thing which results from life in arid regions.

(5) I shall offer evidence below which tends to show that the need for concealing coloration on the part of these rodents has been greatly overestimated.

The general correlation between depth of pigmentation and atmospheric humidity is, of course, a widely recognized fact. Not only may we contrast the pale desert races with their dark relatives from the humid coast belt of the northwest, but various intermediate stations may be chosen, whose birds and mammals display intermediate shades in their feathers and fur.[1a] This principle is not, of course, one of universal application, the correlation in respect to color-tone being very imperfect. Nevertheless, the phenomenon is so widespread and so well known that I need not even cite specific cases in the present discussion.

Now the hypothesis of concealing coloration through natural selection might doubtless be advanced with a certain degree of plausibility to cover this entire situation. It could be pointed out that regions with more humid climates (at least those having a higher rainfall) have darker (appearing) soils than the less humid ones, and that therefore the effective correlation may be between pigmentation and soil color, rather than between pigmentation and humidity *per se*. But the fact that outside of the desert regions the ground, in a state of nature, is commonly covered by vegetation renders such an argument very unconvincing. Green grass is doubtless somewhat darker than dry

[1] See Grinnell (Univ. of California Pub. Zool., vol. 12, p. 257).

[1a] Instances of this tendency among mice are discussed in papers by the present writer, in the American Naturalist (April–May, 1918,) and the Journal of Experimental Zoölogy (April 5, 1920).

grass, but a seal brown mouse would probably be no better concealed in the former than in the latter.

We come now to cases in which narrowly localized races have been described, that are said to harmonize more or less strikingly with some special habitat, in respect to color-tone, and to differ noticeably from their near kin in regions closely adjacent. In some of these cases, at least, the argument that the responsible agent has been optical, rather than atmospheric, assumes a higher degree of plausibility.

Several writers have recorded the existence of very pale races of wild mice upon isolated beaches or sandy islands along the coast.[2] In a previous paper,[3] I have analyzed one of these cases rather carefully. I there dealt with a paler sub-race of *Peromyscus maniculatus rubidus*, inhabiting a practically isolated sandy peninsula on the northern California coast. Through the use of an accurate method of color determination,[4] I am now able to indicate the relative shades of the skins from the peninsula and from the redwood forests of the mainland across Humboldt Bay. The proportion of black in the two cases is 89.0 per cent for the former and 90.9 for the latter. These figures are based upon 21 and 29 mature skins respectively. The difference (1.9 per cent) is not great, but it is about 12 times its probable error ($\pm 0.16$) and therefore cannot be accidental. Furthermore, it is to be remarked that all but one of the peninsula mice show less than 90 per cent of black; while all but three of the redwood mice show more than 90 per cent. Indeed, the difference between the two series is quite evident to the eye, even upon casual inspection.[5]

[2] For instance, Bangs (see Osgood, North American Fauna, No. 28, 1909, p. 121) described such a race from the island of Monomoy on the Massachusetts coast. See, also, interesting recent accounts by G. M. Allen and by A. H. Howell (Journ. Mamm., November, 1920).

[3] American Naturalist, March, 1917; Osgood (Revision of the Genus Peromyscus, p. 66) had already referred to the case in question.

[4] Flat skins, prepared according to a uniform method, and cleaned in benzine, are subjected to color analysis by means of the Hess-Ives Tint Photometer. In the present paper, the figures given represent the average tone of an area of the pelage, 24 mm. wide by 17 long (the dimensions of the visible field) and lying symmetrically, near the posterior end of the dorsal surface. One great advantage of the instrument used is that the area under analysis is rendered perfectly homogeneous and is thus strictly comparable with another homogeneous field which serves as the standard. Later I hope to discuss the use of this instrument in the study of mammalian pelages.

[5] If we consider the percentages of white, rather than of black, we have 9.2 and 8.0 respectively for the two series. This makes the difference 15 per cent of the lesser number. A much smaller increase in the proportion of white upon a color-wheel is very evident to the eye.

I have already reported[6] that these differences appear to be hereditary. Unfortunately, only three specimens of the peninsula stock have been reared at La Jolla, but all of these are paler than the palest of the redwood stock, reared at the same time, and under identical conditions. The mean percentage of black in the three skins is 88.3.

This case may be seized upon in support of the protective coloration hypothesis, but I am still disposed to adopt the view expressed in the paper cited (1917, p. 180): ". . . . it seems more likely that the pale coloration of these mice stands in some more direct relation to the humidity of their immediate surroundings." Referring to the latter, I stated (p. 179): "Despite the nearness to the ocean and the high atmospheric humidity, the peninsula region seems dry in comparison with the redwood forests. This is due in part to the loose, sandy character of the soil—where, indeed, any real soil exists—and to the comparative lack of shelter from the prevailing westerly winds. Evaporation here is doubtless more rapid than in the comparatively stagnant air of the forests." I might have added that the humidity of their subterranean abodes, in which these mice are reared and spend the greater part of their existence, is almost certainly lower in the sandy region.

The case which has chiefly prompted the publication of the present paper is that of the alleged effect of black lava in darkening the pelage of certain rodents and other animals which make it their habitat.

In his well-known "Results of a Biological Survey of the San Francisco Mountain Region and Desert of the Little Colorado, Arizona,"[7] Dr. C. Hart Merriam mentions four different animals which were captured in the lava fields of this district, and which differed strikingly in color from their nearest relatives in the neighboring desert regions. These animals are (using revised nomenclature):

Citellus spilosoma obsidianus
Onychomys leucogaster fuliginosus
Perognathus flavus fuliginosus
Phrynosoma hernandesi

The first, a squirrel, was described as a new subspecies, the second (a true mouse) and the third (a pocket mouse) as new species. The last (a "horned toad") is referred to by Doctor Stejneger, who reported

[6] American Naturalist, March, 1917, June–July, 1918.

[7] U. S. Department of Agriculture. North American Fauna, No. 3. Washington, 1890.

upon the reptiles, as "a melanistic form."[8] In each case, considerable stress is laid upon the dark coloration of the lava-dwelling forms, it being more than once stated that we have to do with "protective coloration."

It may seem to be worse than reckless for one who has neither seen the specimens nor visited the locality under consideration to call in question such circumstantial statements by an eminent naturalist. It should not be necessary for me to explain, however, that the only point at issue is the interpretation of Doctor Merriam's findings. In view of the wholly negative results of my own investigations, to be described shortly, I think that I need offer no apology for questioning whether some interpretation alternative to that adopted by Doctor Merriam is not possible here.

Two such alternatives suggest themselves. The first of these is that the color correspondences observed were due to accident. Mice of the same species and subspecies are known to vary widely in color, pale and dark specimens being trapped in the same neighborhood. One may readily form premature conclusions from an insufficient number of specimens, owing to "errors of random sampling." In the present case, it is to be noted that the first of the four named species was represented in Doctor Merriam's collections by two specimens, the second by five (two being listed as "somewhat intermediate"), the third by a single specimen, and the last by two. Moreover, several of the specimens (including the single *Perognathus*) are listed as "immature," a circumstance which raises the question whether the darker shade of the pelage was not due, in part at least, to this fact.

One would naturally lay less stress upon this first alternative explanation, particularly since Mr. Vernon Bailey (as he informs me) is able to corroborate from his own observation these impressions regarding the darker pelage of certain rodents of the region in question.

A second possibility seems to be more worthy of consideration. It is to be noted that in the case of the mammals, at least, the darker race was taken in the "piñon and cedar belt," while the paler race, with

[8] It must be insisted that the case of the reptiles is quite different from that of the mammals in respect to adaptive coloration. Some lizards, as is well known, have chromatophores which are under the direct control of the nervous system, and are therefore capable of fairly rapid color adjustments. It may well be that many other species possess this power to a less striking degree. On the other hand, it would hardly be claimed that mammalian hair is subject to such influences.

which it was compared, came from the Desert of the Little Colorado. Now it is evident from both the maps and the text of the report, that the former region occupies a considerably higher altitude than the latter, there being an average difference of more than a thousand feet between the two. Indeed they are assigned to different life zones. While no meteorological records are accessible to me, it seems very probable that the precipitation in this belt of piñons and junipers on the mountain slopes is considerably greater than on the desert plains below. Are we, then, justified in eliminating humidity as the responsible factor in bringing about the color differences in these two localities? Or is it not, indeed, possible that some unknown third factor is the one chiefly concerned?

Certain other opinions regarding the effect of lava in determining the colors of rodents should be referred to before leaving this discussion. W. H. Osgood, in his valuable "Revision of the Mice of the American Genus Peromyscus"[9] tells us (page 16) that "if the range of a given form includes a few square miles of lava beds, specimens from that area show an appreciably darker color than the normal form occupying the surrounding region." Again (p. 70) "in northeastern California, the mice of the semidesert lava beds are more like the dark *gambeli* than the pale *sonoriensis*. Throughout the desert region *sonoriensis* is the prevailing form, except on the lava beds."

It is unfortunate that more specific instances are not given in support of these statements. We should like to know more of the rainfall, vegetation, etc., of these lava beds of northeastern California; likewise (and this is vitally important) their distance from regions in which true *gambeli* is abundant. Some of Osgood's other statements (pp. 16, 70) regarding the effects of narrowly localized environmental differences, apparently in the absence of any form of isolation, are not supported by the experience of various other collectors. They must, I think, merely voice impressions based upon accidental coincidences. The careful experiments of H. H. Collins (not yet published) show that the more marked color differences, occurring in a given locality within the range of a single subspecies, are hereditary and not due to any immediate environmental influence.

Goldman[10] has recorded observations similar to those of Osgood. Of one wood-rat, *Neotoma intermedia desertorum*, he writes (p. 77):

[9] U. S. Department of Agriculture. North American Fauna. No. 28. Washington, 1909.

[10] Revision of the Wood Rats of the Genus Neotoma. U. S. Department of Agriculture, North American Fauna, No. 31. Washington, 1910.

"Specimens taken in lava beds are usually darker than those inhabiting lighter-colored rock formations." Similar statements are made in respect to other species on pages 81 and 102. Unfortunately, we have no record of the number of individuals on which these statements are based, save that in the case of *N. lepida stephensi* but a single specimen was recorded from the lava beds. We likewise have no information as to the altitude, meteorological conditions, etc., of the particular lava fields where the species in question were trapped.

The chief direct evidence which I have to offer on the present subject was obtained during a collecting trip undertaken in the spring of 1920. The choice of locality was due primarily to the suggestions of Prof. Joseph Grinnell, director of the University of California Museum of Vertebrate Zoology. Doctor Grinnell, succeeded by Mr. Richard Hunt, of the same museum, together with the writer, constituted the field party.

The lava field on which the mice were trapped lies in the Mojave Desert some 12 miles west of the village of Ludlow, and just south of the main line of the Santa Fe Railway. Unfortunately, no Geological Survey or other reliable map of this region exists. The outline of the field is very irregular, the greatest length being perhaps five miles and the greatest width three.

Regarding the age of this eruption I can learn nothing definite. The lava, throughout much of the area, looks extremely fresh, and a beautifully preserved cinder-cone ("Mt. Pisgah") occurs near the northern border. On the other hand, there are, so far as I know, no hot springs, fumaroles or other evidences of recent volcanic activity in this part of the desert. Whether the age of the field is to be reckoned in hundreds or in thousands of years I am unable to learn from the geologists whom I have consulted.

The surface of this lava bed is raised well above the general level of the desert. It is extremely rugged and difficult of passage, being crossed in every direction by jagged ridges and yawning fissures. Sand has drifted in from the surrounding desert and become deposited in cracks and depressions, affording soil for the support of scattered shrubs and annuals, even a mile or more from the nearest border. Despite the presence of occasional sand pockets of considerable extent, the prevailing tone of the lava field is extremely dark. Viewed from neighboring hilltops it everywhere stands in extreme contrast to the pale sand and gravel which surrounds it on every side. Furthermore, it must be emphasized that the mice are not confined to the small

areas of pale sand, but appear to wander freely over the barest and blackest masses of lava rock, in which positions they were frequently trapped.

Preliminary trapping revealed the fact that there were several species of mice on this field. By far the most frequent was *Peromyscus crinitus stephensi*, but *P. maniculatus sonoriensis* and two species of *Perognathus* were met with.

Circumstances pointed to the first of the foregoing species as being best adapted for the test which I had in view. As is well known, this mouse shares the prevailing buff or sandy hue so characteristic of desert rodents. Furthermore, it has one very great advantage for present purposes, namely, that it is restricted in its habitat to rocky regions, in the crevices of which it finds its shelter. Here, then, we seemed to have the conditions favorable for a crucial natural experiment. This rather extensive lava field was surrounded on all sides by areas of sand and fine gravel. Trapping, undertaken to test this point, revealed the fact that the *crinitus* mice rarely, if ever, left the lava beds and strayed for any distance into the open desert. Live-traps, which I set for 175 "trap nights"[11] upon the desert areas adjacent to the lava field yielded but two specimens of *crinitus*, both of these within 150 feet of the lava. Furthermore, Mr. Hunt, during two weeks' use of spring traps in this region, did not catch a single specimen of this species away from the lava beds. In contrast to these negative results, it must be pointed out (1) that large numbers of mice of other species were taken in these sandy areas, and (2) that *crinitus* was extremely common throughout the lava field, where it predominated over all other small rodents. It would seem likely that for centuries, and perhaps for a vastly greater period, this colony of *Peromyscus crinitus stephensi* had been isolated by fairly rigid barriers from other mice of the same species.[11a] Since the statements of Merriam, Osgood and Goldman, cited above, relate to species and to localities concerning which no such claim of isolation is advanced, it would seem that in

[11] This useful unit of trapping activity is due to Grinnell (An Account of the Mammals and Birds of the Lower Colorado Valley, University of California Publications in Zoology Vol. 12, 1914, p. 92).

[11a] Doctor Grinnell suggests that "periodic eruptions" of these mice, due to over-population, might carry them, from time to time, across these barriers. I can only reply (1) that we have no knowledge of such migrations here; (2) that such a diffusion process is at least as likely to occur in those localities where a darkening effect of lava has been alleged.

the present case, if anywhere, the darkening effect of the lava would manifest itself.

Five hundred and thirteen trap nights on the lava field yielded me 157 specimens of *crinitus*, along with 23 specimens of mice of other species. From the former rather more than fifty skins were prepared. No selection whatever was made in choosing the individuals for skinning, save that mice with immature or with badly damaged pelage were rejected, while many others were unavailable owing to early decomposition.

The first results of this trapping made it plain that these mice belonged to no specially modified lava-dwelling race. They had retained the pale brown-gray hue, sprinkled dorsally with black, so familiar to us in desert rodents generally. When laid upon the dark lava rocks, they certainly could not be called inconspicuous, as the accompanying figure shows. (Plate 6.)

The fact that this seemingly conspicuous rodent flourishes in such numbers upon these lava fields gives us good ground for skepticism as to the need for concealing coloration among closely related species. And it surely justifies us in challenging those who assume without evidence the existence of a selection so rigid that trifling differences in shade are of frequent survival value.

It should also be mentioned here that none of the other species of mice and rats which were trapped upon this lava field by Mr. Hunt and myself gave any evidence of modification in the direction of deeper pigmentation. The species taken comprised one other *Peromyscus*, two species of pocket mice and a wood-rat. While no extensive series of skins was prepared for these other species, any very pronounced darkening would doubtless have been observed. With a single possible exception, the only noticeably dark pelages were those of juvenile specimens.

Although it was evident that no considerable degree of darkening had occurred among these lava-dwelling representatives of *Peromyscus crinitus*, the question still remained whether there had been any modification whatever, which might be revealed by careful quantitative methods. For this purpose a control set of specimens was necessary.

The control series I should naturally have collected in the Bullion Mountains, a rocky range, a few miles to the southwest, in which I knew that these mice occurred. But the presence of another extensive lava field upon the nearby slopes of this range, was regarded as com-

plicating the situation.[12] We therefore moved to a considerably more distant point. The spot chosen was a rocky range of hills near the village of Oro Grande, on the Mojave River, between fifty and sixty miles to the westward of our previous station. The new locality was some seven or eight hundred feet higher than the previous one, and perhaps differed somewhat climatically, as it did in respect to vegetation. It was, however, a typical stretch of desert country, and many of the more abundant plant species were common to the two regions. The hills along the base of which we trapped were covered with large masses of igneous rock, whose prevailing hues were pale gray, buff and pinkish, interspersed with areas of finer materials (gravel and sand) of a still paler hue. No lava fields or other extensive masses of dark rock occur in this vicinity.

One hundred and thirteen specimens of *P. crinitus*, together with thirteen belonging to other species, were taken in my live-traps in the course of 478 trap nights. Fifty skins were preserved, care being exercised, as before, that the choice of individuals should bear no relation to the color of their pelage.

A superficial comparison of this series of skins with that from the lava field revealed no obvious difference in their average color-tone. A careful quantitative study confirms this first impression. Indeed it seems rather remarkable that two random collections comprising such limited numbers, should agree so closely. The mean readings of the two series,[13] through the three color-screens of the Hess-Ives Tint Photometer, are as follows:

| | RED | GREEN | BLUE-VIOLET |
|---|---|---|---|
| Lava | 26.2 | 19.2 | 16.0 |
| Oro Grande | 26.7 | 19.4 | 15.9 |

[12] This second field is rather more than a mile distant (at the nearest point) from the "Pisgah" lava bed on which the trapping was done. The intervening area was occupied by level ground, entirely devoid of rock and likewise apparently of *Peromyscus crinitus*. Elsewhere, the "Pisgah" field is separated by much wider intervals from the nearest rocky hills.

[13] A few skins were rejected from each series owing to immaturity, or to obvious loss of hair. There remained 45 in the lava set, 46 in that from Oro Grande.

Reduced to terms of black, white, and color (in this case a shade of yellow) we have:[14]

| | BLACK | WHITE | COLOR |
|---|---|---|---|
| Lava | 79.8±0.19 | 16.0 | 4.2 |
| Oro Grande | 79.6±0.18 | 15.9 | 4.5 |

The trivial excess of black in the lava series is of no statistical significance, as appears from the fact that this difference is less than its probable error. It is to be noted that the lava series likewise shows a trivial excess of white, which is further evidence of the "accidental" character of all these slight differences between the two sets of figures.

Various objections may perhaps be brought forward by critics to the propriety of drawing any general conclusions from this single instance which yielded negative results. It will perhaps be pointed out that I have dealt with a wholly nocturnal animal. I should, it may be urged, have chosen some diurnal species, for which concealing coloration would be more necessary. In reply, I need only remark that two of Doctor Merriam's species (the *Onychomys* and the *Perognathus*) are as completely nocturnal in their habits as is *Peromyscus crinitus*, while the remarks of both Osgood and Goldman likewise apply to nocturnal species.

It may be urged, too, that the lava fields on which I have trapped my specimens are of unknown age and that they are perhaps much more recent than those of the San Francisco Mountain district. I cannot, I confess, meet this argument directly. It is certainly pertinent to point out, however, that the pale *crinitus* mice of this Mojave Desert lava field still succeed in maintaining themselves in great abundance, after a period which is certainly to be measured in centuries, and perhaps by even greater periods of time. This fact does not harmonize well with the assumed rigid selection on the basis of color-tone.

Another objector may insist that *Peromyscus crinitus* may, by reason of special habits, have no need for protective coloration, whereas the same may not be true of various other rodents. This, indeed, is quite possible. If it be true, however, we may well query why this species

[14] Those who have had no experience in color analysis may be surprised by my characterizing as "pale" a shade containing nearly 80 per cent of black. I will merely point out that a piece of faded khaki which I tested gave photometer readings very close to those for these mouse skins, but that the former was slightly darker.

has ever adopted the familiar pale hue, which seems to be an adjustment to the prevailing tones of the desert at large. Either way we take it, the argument seems to lead us into difficulties.

I am prepared, too, for the disparaging comments of such biologists as regard the experimental method as the only key to scientific truth. All this field observation, I may be told, is beside the mark. I should have subjected my animals to experimental tests in the laboratory. As a matter of fact, I have done this very thing, not with *Peromyscus crinitus*, to be sure, but with various subspecies of *maniculatus*. I have thus far found no evident tendency toward convergence on the part of these several races, even after a considerable number of generations in captivity under identical life conditions. Possibly photometer tests of prepared skins will reveal a slight change of color, but this is not yet obvious to the eye. The direct effect of humidity or other physical agents upon pigmentation, if such exists, must manifest itself very gradually in the case of these mice.

In conclusion, let me say that I make no claim that the single case which I have studied intensively affords a disproof of the effect of a lava background upon the coat color of every other mammal. But I do urge that the wholly negative result derived from this seemingly critical case, gives ground for reasonable skepticism, and that it throws the burden of proof upon those who have, thus far, offered us merely generalized impressions or very limited data.

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*Peromyscus crinitus stephensi* FROM LAVA FIELD, SEEN AGAINST A BLOCK OF DARK LAVA

Skin prepared by R. Hunt; photograph by H. R. Fitch. Reduced. The lighting conditions make the anterior half of the mouse appear somewhat too pale. Mus. Vert. Zool., no. 31393.